LEFT POSTERIOR PARIETAL CORTEX PARTICIPATES IN BOTH TASK PREPARATION AND EPISODIC RETRIEVAL

by

Jeffrey S. Phillips

B.A., Villanova University, 1997

Submitted to the Graduate Faculty of

the School of Arts & Sciences in partial fulfillment

of the requirements for the degree of

Master of Science

University of Pittsburgh

2009

UNIVERSITY OF PITTSBURGH

SCHOOL OF ARTS & SCIENCES

This thesis was presented

by

Jeffrey S. Phillips

It was defended on

July 10, 2008

and approved by

Dr. Julie A. Fiez, Professor, Department of Psychology

Dr. David A. Wolk, Assistant Professor, Department of Neurology

Thesis Director: Dr. Mark E. Wheeler, Assistant Professor, Department of Psychology

LEFT POSTERIOR PARIETAL CORTEX PARTICIPATES IN BOTH TASK PREPARATION AND EPISODIC RETRIEVAL

Jeffrey S. Phillips, M. S.

University of Pittsburgh, 2009

Optimal memory retrieval depends not only on the fidelity of stored information, but also on the attentional state of the subject. Factors such as mental preparedness to engage in stimulus processing can facilitate or hinder memory retrieval. The current study used functional magnetic resonance imaging (fMRI) to distinguish preparatory brain activity before episodic and semantic retrieval tasks from activity associated with retrieval itself. The use of a catch-trial imaging paradigm permitted separation of neural responses to preparatory task cues and memory probes. Episodic and semantic task preparation engaged a common network, including the bilateral intraparietal sulcus (IPS), left fusiform gyrus (FFG), and pre-SMA. In the subsequent retrieval phase, the left IPS participated in a frontoparietal network which responded differentially to old and new stimuli. In contrast, the right IPS was influenced only by preparatory cues, with minimal modulation during memory retrieval. Preparatory activity in the left IPS and its sensitivity to old/new differences indicate that this brain region participates both in task preparation and in episodic retrieval. This dual response profile suggests the left IPS as a possible interface between systems for domain-general attentional control and episodic retrieval.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PREFACE

This research was supported by the Learning Research and Development Center at the University of Pittsburgh (NIH grant NS46424) and the Multimodal Neuroimaging Training Program (NIH/NIDA grant T90 DA022761) of the Center for the Neural Basis of Cognition.

Personally, I would also like to acknowledge my parents for the encouragement they have provided, and Nina Clements for her interest and empathy.

1.0 INTRODUCTION

Previous memory research has demonstrated that a person's attentional state during memory retrieval can affect the success and efficiency of retrieval. Attentional states conducive to episodic retrieval in general, or to specific retrieval conditions, have been referred to as *retrieval mode* and *retrieval orientations*, respectively (Tulving, 1983, 2004). Neuroimaging findings suggest that preparatory cues indicating the nature of retrieval operations to be performed can facilitate the adoption of a retrieval mode or appropriate retrieval orientations (e.g., Rugg and Wilding, 2000; Herron and Wilding, 2004). Preparation for retrieval can be interpreted in terms of task-level rules and strategies: when cues provide no information about specific retrieval targets, subjects can prepare by bringing to mind the decision criteria required by the task, response options, and useful criteria for filtering information in memory. Task-level control processes can be difficult to dissociate from stimulus-level retrieval processing, since the two occur in conjunction.

Much of the neuroimaging evidence supporting task-level preparation for memory retrieval comes from studies of event-related potentials (ERPs). These studies have demonstrated that cues signaling episodic and semantic retrieval tasks produce differential patterns of brain activity (Düzel et al., 1999; Herron and Wilding, 2004; Morcom and Rugg, 2002), supporting the hypothesis that subjects adopt an appropriate retrieval mode prior to an

act of retrieval. Preparatory brain activity not only differs between episodic and semantic retrieval, but also between different episodic retrieval tasks (Dobbins and Han, 2006; Herron and Wilding, 2004; Werkle-Bergner et al., 2005).

To date, the number of functional magnetic resonance imaging (fMRI) studies investigating preparatory processes in episodic retrieval has been relatively small. While studies using fMRI and positron emission tomography (PET) have linked sustained brain activity during episodic retrieval with the concept of a retrieval mode (Buckner et al., 1998a; Düzel et al., 1999; LePage et al., 2000; Nyberg et al., 1996; Velanova et al., 2003), these studies have not distinguished initial preparation for retrieval from the effects of repeated task performance. Other fMRI investigations by Dobbins and Han (2006) and Velanova et al. (2007) have distinguished between early preparation and later retrieval-phase processing, but neither of these studies contrasted episodic retrieval with other task conditions. The current study thus investigates brain activity associated with preparation for episodic vs. non-episodic retrieval tasks, in order to identify neural mechanisms which may be involved in the initial adoption of an attentional state appropriate to episodic retrieval.

In the current paradigm, we make use of a catch-trial fMRI design (Ollinger et al., 2001a, b; Shulman et al., 1999; Wheeler et al., 2006) to temporally dissociate brain activity related to task vs. memory retrieval. During scanning, participants alternated between old/new recognition memory trials (episodic retrieval) and living/non-living decision trials (semantic retrieval). Preparatory phase brain activity was associated with the presentation of task cues which provided no information about upcoming memory probes, but which communicated task-level information about response options and decision criteria (Fig. 1). In contrast, retrieval phase

brain activity was associated with the presentation of memory probes and subjects' subsequent behavioral response. Processing during this period is likely to include brain activity directly related to memory retrieval, as well as general attentional control processes involved in goal maintenance, decision making, and response selection and execution.

We reasoned that attentional control regions involved in task preparation should exhibit robust responses to preparatory cues. We hypothesized that preparation would modulate activity in parietal and posterior temporal areas that have been found to be responsive during preparation to retrieve sensory-specific information (Wheeler et al., 2006) and to make sensory discriminations (Shulman et al., 1999). Additionally, we sought to separate retrieval phase activity related to attentional control vs. memory retrieval by its sensitivity to old/new stimulus differences. Regions involved in putative retrieval processing should be sensitive to the study history of stimuli (Donaldson et al., 2001a) and should exhibit greater responses to previously studied items. In contrast, regions involved in post-stimulus attentional control processes would be insensitive to study history.

2.0 MATERIALS AND METHODS

2.1 PARTICIPANTS

Participants were nineteen right-handed native English speakers with normal or corrected-to-normal vision (10 female, mean age 25 years). All participants underwent screening for conditions which would preclude behavioral participation or present a hazard for participation in an MRI experiment. Four participants were excluded due to excessive head motion (greater than 3 mm), failure to complete the study, or scripting errors. Three additional participants were excluded due to chance-level performance in the old/new recognition task. All remaining participants (n=12) provided 8-10 runs of data, depending upon available time. Participants gave informed consent as required by the Institutional Review Board of the University of Pittsburgh and were paid $75 for their participation.

2.2 MATERIALS

Stimuli were 480 English nouns obtained from the MRC Psycholinguistic Database (http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Stimuli were between 4 and 8 letters in length, with Kucera-Francis written frequencies (Kucera and Francis, 1967) from 1 to 787

instances per million. The stimulus set was divided into 240 words representing living things (mean frequency=34 instances/million) and 240 words representing non-living things (mean frequency=48 instances/million). For each participant, 96 "living" items and 96 "non-living" items were randomly selected to produce a study set of 192 words. Equal numbers of items were randomly selected from living and non-living lists for presentation as unstudied items in the scanned episodic and semantic retrieval tasks. Order of stimulus presentation was randomly determined. Words were displayed in capital letters in 12-point black Helvetica font on a white background.

2.3 EXPERIMENTAL PARADIGM

The scanned test phase used a fast event-related task-cueing paradigm in which participants engaged in pseudorandomly ordered trials of episodic (old/new recognition memory) and semantic (living/non-living) retrieval tasks. For each subject, 10 runs of 177 image acquisitions each were prepared. The factors of task (episodic or semantic judgment), animacy (living or non-living word), and study history (old or new word) were orthogonally manipulated to yield 4 trials per run of each combination of factors. In all experimental trials, participants saw a centrally-presented task cue ("OLD OR NEW" or "LIVING OR NON") for 500 ms, followed by 1500 ms of central fixation before the appearance of the probe word (Fig. 1). Each probe word appeared on screen for 500 ms, followed by 3500 ms of fixation, during which subjects were to respond. At the end of this period, the fixation cross turned red for 500 ms to indicate the end of the trial.

These "compound" (preparatory cue + memory probe) trials comprised 80% of experimental trials. Compound trials were pseudorandomly intermixed with "catch" trials (Fig. 1), in which a task cue was followed by 1500 ms of fixation and the trial-end signal (red fixation cross), without the intervening presentation of a test item. Catch trials allowed separation of hemodynamic responses associated with preparatory and retrieval phases of experimental trials (Ollinger et al., 2001a, b; Shulman et al., 1999; Wheeler et al., 2006). Four episodic-cue and four semantic-cue catch trials were included in each run. This proportion is within the range recommended by Ollinger and colleagues. The pseudorandom ordering of conditions was determined using an automated algorithm which ensured that a given trial type was equally likely to be preceded by every other trial type (Buckner et al., 1998b). To allow deconvolution of the hemodynamic response, randomly distributed inter-trial intervals (ITIs) of 1500, 3500, and 5500 ms were used; the distribution of these ITIs was exponential, with more ITIs of shorter duration (Dale, 1999).

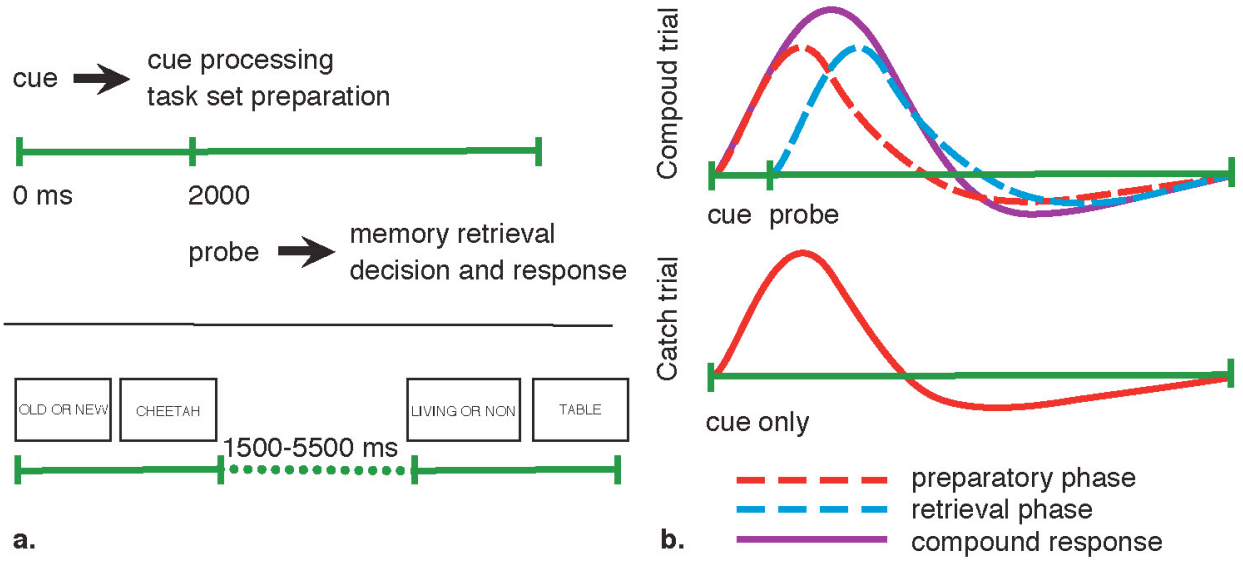

Figure 1. Schematic representations of task and catch-trial design

Fig. 1a: Overview of trial structure and hypothesized cognitive processes engaged by task preparation and performance. In the preparatory phase, participants were shown either an episodic ("OLD or NEW") or semantic ("LIVING or NON") task preparatory cue for 500 ms, followed by a constant fixation interval of 1500 ms. Preparatory activity is thought to reflect cue processing and task-level preparation, including self-reminding of task goals, decision criteria, and response options. Retrieval phase activity is associated with search of and retrieval from declarative memory, as well as decision-making and response processes. Fig. 1b: Neural responses to preparatory cues and memory robes were independently modeled using a catch-trial design. Compound trials (preparatory cue + memory probe) comprise 80% of trials; catch trials (cue only) comprise 20 percent. Inclusion of catch trials allows sufficient variability to separate cue and probe responses in GLM analysis (Ollinger et al., 2001a, b; Shulman et al., 1999; Wheeler et al., 2006).

2.4 IMAGE ACQUISITION

All images were acquired on a 3-Tesla Siemens Allegra magnet at the University of Pittsburgh's Brain Imaging Research Center. Prior to functional imaging, a T1-weighted high-resolution magnetization prepared rapid gradient echo (MP-RAGE) image (192 parasagittal slices; 1 mm^3 voxels; repetition time (TR)=1540 ms; echo time (TE)=3.04 ms; flip angle=8; inversion time=800 ms) and a T2-weighted in-plane anatomical image (35 oblique axial slices parallel to anterior commissure-posterior commissure (AC-PC) line; in-plane resolution=0.8 mm x 0.8 mm; slice thickness=3.2 mm; TR=5780 ms; TE=73 ms; flip angle=150) were acquired. Functional images were collected with a $T2^*$-weighted echo-planar pulse sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (Kwong et al., 1992; Ogawa et al., 1992) in the same

orientation as anatomical images (in-plane resolution=3.2 x 3.2 mm; slice thickness=3.2 mm; TR=2000 ms; TE=30 ms; flip angle=79). The first five image acquisitions per run were discarded to allow net magnetization to reach steady state. No trials were performed during the last nine image acquisitions of each run, allowing time for the BOLD response to return to baseline.

2.5 PROCEDURE

Prior to the scanning session, participants studied a list of 192 words, which they were instructed to remember for an upcoming memory test. Words were presented serially on a computer monitor for 3 s each, and participants were told that they would not be asked to recall the order of presentation, only whether a word had been studied or not. After each word disappeared from the screen, participants pressed the space bar to advance to the next word. Following the study session, a full explanation of the episodic and semantic tasks was given, and participants performed a brief practice block using words from outside the experimental set. In the practice session, participants were instructed to pay attention to the task cue on each trial and to respond by making one of two keypresses (old/living or new/non-living). Participants were informed beforehand of the occurrence of catch trials and the reason for their inclusion.

Scanning began approximately 45 minutes after study and instruction phases. Stimuli were presented using PsyScope X (Cohen et al., 1993; http://psy.ck.sissa.it) on a Macintosh PowerBook G4, and were projected from the rear of the scanner to a mirror positioned above participants' eyes. Participants held a button stick in either their left or right hand and were

instructed to respond by pressing the index or middle finger buttons. Response hand was counterbalanced across participants. In all cases, the index-finger button corresponded to living and old responses, while the middle-finger button corresponded to non-living and new responses. Data were scored for accuracy and assigned to separate conditions based on study history (old, new), task (episodic, semantic), and accuracy (correct, incorrect). Trials with RTs < 300msec were discarded from behavioral analysis.

2.6 FUNCTIONAL MRI DATA ANALYSIS

Participants' imaging data were corrected for head motion within and across runs using a rigid-body algorithm with 3 translational and 3 rotational parameters (Snyder, 1996). Whole-brain adjustment normalized the modal voxel value for all participants to a value of 1000 to allow comparison between datasets (Ojemann et al., 1997). A sinc interpolation corrected for between-slice differences in acquisition time, re-aligning all slices to the first slice. Data were resampled into 2 mm isotropic voxels and transformed to the Talairach and Tournoux (1988) reference space.

Data were analyzed at the voxel level with the general linear model (GLM; Friston et al., 1994; Miezin et al., 2000). Analysis was performed using the FIDL software package, developed at Washington University, St. Louis (Miezin et al., 2000; Ollinger et al., 2001a, b). GLMs for each participant were smoothed with a 4mm Gaussian filter. For each run, a trend term was used to regress out the influence of scanner signal drift over each term, while a constant term modeled

the baseline signal. Timecourses for each condition of interest were estimated by a deconvolution analysis, which makes no assumptions regarding the shape of the hemodynamic response.

BOLD responses to preparatory cues and memory probes (Fig. 2) were modeled separately using the method employed by Wheeler et al. (2006). Preparatory responses were time-locked to the onset of task cues and coded into the GLM design matrix with a series of 10 delta functions, one for each functional volume collected in the 20 s following onset of the preparatory cue. To obtain an estimate of the preparatory phase response, catch-trial cues were coded together with cues occurring in compound trials. Retrieval phase responses were time-locked to the onset of memory probes and were coded with a series of 9 delta functions, comprising 9 functional volumes (18 s) after the onset of test words. On compound trials, in which preparatory cues were followed by memory probes with a stimulus-onset asynchrony of 2 s, modeling of the preparatory phase response thus began 1 TR before modeling of the retrieval phase response.

While the cue-probe interval was held constant, between-trial intervals varied between 1500 and 4500 ms (Fig. 1). By jointly including catch trials and jittering inter-trial intervals, we created sufficient variability to allow independent estimation of preparatory and retrieval phase responses. GLM coding distinguished episodic and semantic preparatory cue responses; retrieval phase responses were separated by retrieval task, study history of memory probes (old vs. new), animacy of the probe's referent (living vs. non-living), and response accuracy (correct vs. incorrect).

2.6.1 Analysis of Preparatory Phase Timecourses

Analysis of preparatory phase conditions aimed to identify regions involved in task preparation. Data from the preparatory phase were entered into a 2 x 10 voxelwise repeated measures ANOVA, with two levels of cue type (episodic, semantic) and 10 levels of time. Subject was treated as a random effect. This analysis produced a main effect of time image, identifying voxels in which brain activity significantly changed from baseline, independently of cue type, over the ten volumes of the preparatory phase timecourse. The analysis also produced an interaction of cue type by time image, which identifies voxels in which activity differs over time as a function of cue type. To identify voxels involved in task preparation, independently of task, we examined regions of interest (ROIs) from the preparatory phase main effect of time map. This map was thresholded at a value of $z > 6.0$, and a mask image was applied to exclude peaks which did not surpass sphericity and multiple comparisons corrections. The multiple comparisons correction employed a minimum cluster extent of 45 voxels to achieve an adjusted alpha level of $p<0.05$, based on previous Monte Carlo simulations conducted by McAvoy et al. (2001). An automated algorithm was used to define ROIs around local maxima. Peaks separated by less than 10 mm were consolidated into the same region of interest. ROIs included voxels which fell within a 10 mm radius of a peak. Region coordinates are listed in Table 4.

Given past observations of both memory-related effects and attentional modulations in posterior parietal cortex (Astafiev et al., 2003; Corbetta et al., 2000, 2002; Kusunoki et al., 2000; Wheeler and Buckner, 2003, 2004), we selected 4 regions in bilateral intraparietal sulcus (IPS) for further analysis: in the left hemisphere, preparatory cues significantly modulated activity in the

anterior (x=-34, y=-47, z=37; BA 7/40) and middle (x=-27, y=-58, z=43; BA 7/40) IPS; in the right hemisphere, robust responses were observed in the middle (x=29, y=-62, z=37; BA 7/19) and posterior IPS (x=32, y=-64, z=47; BA 7). Because sensitivity to the cued task would suggest candidate regions supporting task-set preparation and implementation, we identified additional regions of interest from the main effect of time image that were differentially modulated by episodic and semantic preparatory cues. For each region, preparatory cue differences were assessed over volumes 4-6 (8-12 s from preparatory cue onset), corresponding to the peak of the hemodynamic response across all conditions. Statistical significance was tested using a single-factor ANOVA and an alpha level of 0.05. Regions displaying significant cue-type differences were selected for further analysis.

2.6.2 Analysis of Retrieval Phase Timecourses

We additionally aimed to identify regions which were engaged by episodic and semantic retrieval. We reasoned that brain areas which were sensitive to the content of episodic memory would exhibit differential responses to old and new memory probes. To generate maps, a 2 x 2 x 9 voxelwise repeated measures ANOVA was performed on task phase data, with two levels of task (episodic, semantic), two levels of study history (correct old, correct new) and 9 levels of time. This analysis produced a set of main effect and interaction images. We used the main effect of time image to identify regions (see methods in previous section) which responded only during the retrieval phase, and which were thus unaddressed by analysis of preparatory phase

timecourses. In selecting preparatory and retrieval phase ROIs for further analysis and presentation, we compared voxel overlap between the two sets of regions. Preparatory and retrieval phase ROIs reported below did not spatially overlap with one another.

ROIs were submitted to a 2 x 2 ANOVA, including the factors of task (episodic/semantic) and stimulus study history (old/new). As in preparatory phase analysis, significance tests employed an alpha level of 0.05 and were performed on the average response over volumes 4-6 of retrieval phase timecourses (8-12 s from memory probe onset). Only correct trials were included in retrieval phase analysis, since error trials might correspond to periods of inattention, confusion about task demands, or motor error.

3.0 RESULTS

3.1 BEHAVIORAL RESULTS

Table 1. Accuracy rates for episodic and semantic tasks

	Episodic task		Semantic task	
	OLD	NEW	LIVING	NON-LIVING
Mean acc. (%)	81	72	96	94
Std. dev. (%)	15	22	3	4

Relatively high accuracy rates in both episodic and semantic retrieval tasks (Table 1) indicate that subjects attended to preparatory cues, as required by the experimental paradigm. Participants performed near ceiling in the living/non-living task: accuracy in all stimulus categories was greater than 90 percent, and an ANOVA including the factors of animacy (living, non-living) and study history (old, new) returned no significant effects. The few errors committed in semantic retrieval probably reflect either unintentional button-presses or responses to ambiguous stimuli (e.g., body parts, or words which could indicate either animals or food products). In the episodic task, participants reliably discriminated between old and new words in the episodic task, with a mean d' of 1.6. Overall, participants recognized 81% of old words, while correctly rejecting 72% of

new words. This apparent effect of study history was non-significant [$F(1,11)=1.369$, $p<0.3$]. The main effect of animacy [$F(1,11)=4.608$, $p < 0.06$] and the interaction of animacy with study history [$F(1,11)=3.572$, $p<0.09$] were marginal but non-significant.

Table 2. Response times for episodic and semantic tasks

	Episodic task				Semantic task (correct trials only)			
	OLD		NEW		OLD		NEW	
	Correct	Incorrect	Correct	Incorrect	LIVING	NON-LIVING	LIVING	NON-LIVING
Mean RT (ms)	1516	1856	1775	1914	1334	1351	318	1303
Std. dev. (ms)	282	324	408	538	252	205	80	226

Mean response times for both tasks are shown in Table 2. Given participants' near-ceiling performance in the semantic task, only RT data for correct trials were subsequently analyzed in this task. Neither old/new differences [$F(1,11)=2.744$, $p<0.1$] nor living/non-living differences [$F(1,11)=0.001$, $p<0.98$] had a significant main effect on semantic task response times. The interaction of study history and animacy approached but did not achieve statistical significance [$F(1,11)=0.980$, $p<0.1$]. Similarly, in episodic task RT data, no main effect of animacy and no interactions involving animacy were found. The factor of animacy was thus dropped from subsequent analysis. While accuracy data had revealed no significant effect of study history, RT data indicated that recognition decisions to old items were significantly faster

than those to new items [$F(1,11)=6.1$, $p<0.05$]. A significant effect of response accuracy on RT was also found [$F(1,11)=11.4$, $p<0.01$], indicating that participants responded more quickly on correct than incorrect trials. No interaction between the factors of study history and response accuracy was found [$F(1,11)=3.2$, $p<0.1$].

Table 3. Response congruency analysis of episodic and semantic task RTs

	Episodic task		Semantic task	
	Congruent	Incongruent	Congruent	Incongruent
Mean RT (ms)	1655	1742	1351	1369
Std. dev. (ms)	301	388	230	240

The maintenance of discrete task sets was partially corroborated by a response congruency analysis. This analysis tests for evidence of irrelevant stimulus processing by contrasting RTs for trials in which old/new and living/non-living decisions would elicit the same motor response with RTs in which the two tasks would have required incongruent responses. The difference between congruent and incongruent trial RTs is interpreted as a measure of the degree to which the uncued task set intrudes upon performance of the cued task. When cued to perform old/new judgments, for example, participants might respond more slowly to stimuli which were old (index finger response) and non-living (middle finger) than to stimuli which were old and living (i.e., when both features map to index finger response). Such RT differences would suggest that processing related to the irrelevant task had created interference in performance of the cued task.

Mean RTs for congruent and incongruent trials in each task are given in Table 3. An ANOVA indicated a significant main effect of congruency [$F(1,11)=5.7$, $p<0.05$], as well as a significant interaction of task and congruency [$F(1,11)=5.7$, $p<0.05$]. While congruent-response trials in both tasks produced shorter mean RTs than in incongruent-response trials, post-hoc t-tests indicated that congruency effects were non-significant in the semantic task [$t(11)=1.1$, $p<0.3$]. In contrast, this effect was much larger (88 ms) in the episodic task and was statistically significant [$t(11)=2.6$, $p<0.05$]. This asymmetric finding indicates that subjects may have considered animacy-related characteristics of stimuli when cued to perform an old/new decision; however, they only performed old/new decisions when instructed to do so. Given the quickness of living/non-living decisions relative to old/new decisions, subjects may have had time to consider the animacy of the memory probe's referent prior to reaching a recognition memory decision. However, a null effect of congruency in semantic trial RTs suggests that when performing living/non-living decisions, participants experienced no interference based on consideration of a memory probe's study history.

3.2 IMAGING RESULTS

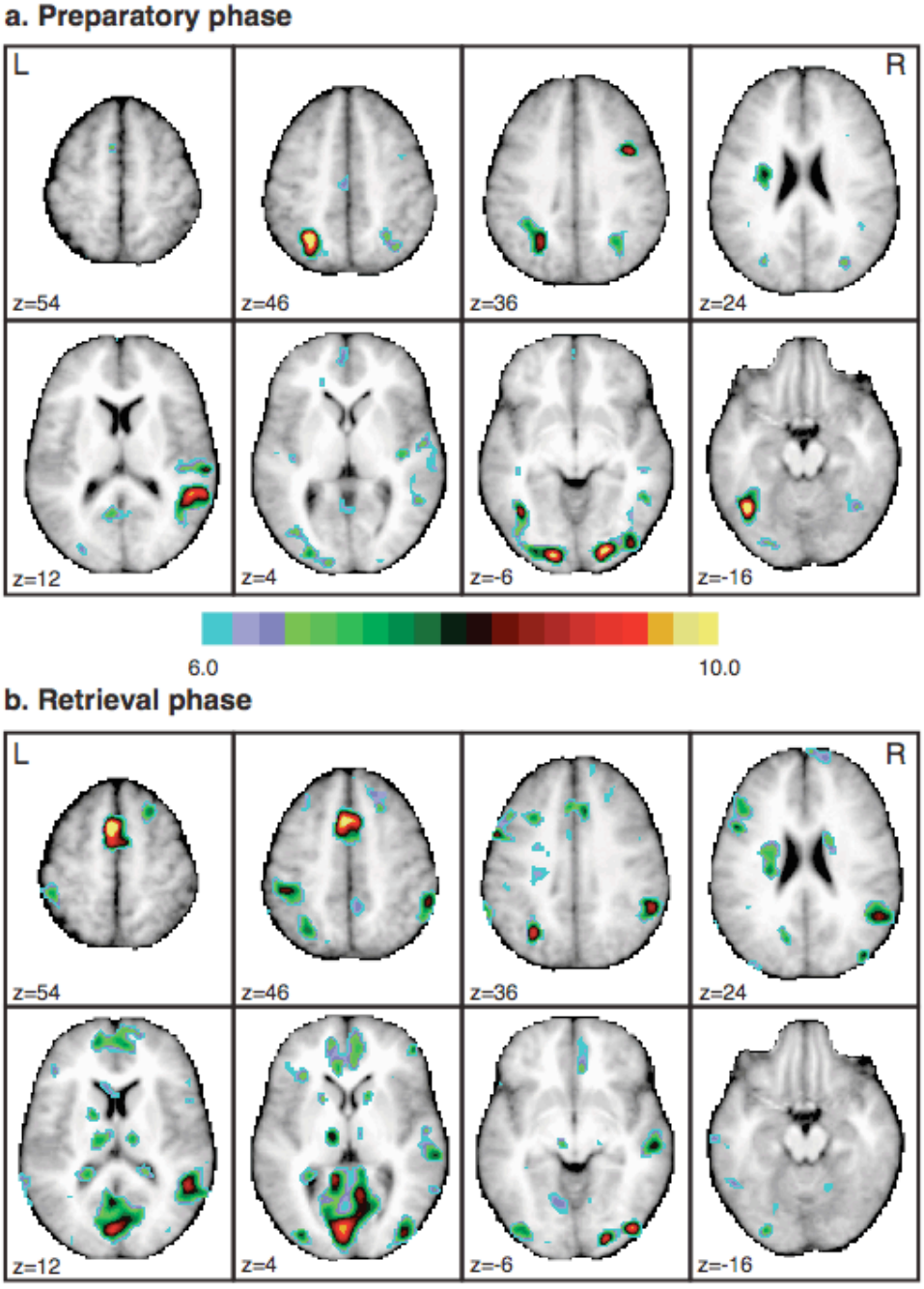

Figure 2. Preparatory and retrieval phase main effect of time maps

Main effect of time maps from preparatory (top) and retrieval (bottom) phases of experimental trials, indicating regions in which activity significantly changed from baseline. Maps shown are uncorrected for multiple comparisons

and thresholded at z>6.0. Regions of interest were defined by masking the uncorrected main effect of time maps with Monte Carlo-corrected, sphericity-adjusted versions of same to exclude peaks which did not meet a corrected alpha-level of 0.05.

3.2.1 Preparatory Phase Effects

The preparatory phase main effect of time map (Fig. 2) revealed widespread, bilateral modulation by preparatory cues. Table 4 lists the peak coordinates of 30 regions displaying the most robust preparatory responses. A full list of regions identified by the main effect of time analysis may be obtained from the authors. Activity encompassed multiple peaks in primary visual, extrastriate, and posterior parietal cortices, as well as midline frontal areas. Notably, several of these peaks correspond to putative loci of attentional or cognitive control, including bilateral intraparietal sulcus (IPS), pre-supplementary motor area (pre-SMA), fusiform gyrus (FFG), and anterior insula (AI). Remarkably similar patterns of activation are reported in Dosenbach et al.'s (2007, 2008) investigations of dynamic and stable task set control, as well as Chein and Schneider's (2005) meta-analytic study of control networks modulated by learning. Preparatory cues signaling episodic and semantic retrieval thus appear to evoke activity in domain-general control areas.

Table 4. Regions defined from preparatory phase main effect of time map

Region	BA	x	y	z	Z-score	Cluster size
L fusiform gyrus	37	-39	-60	-15	11.1	472
L middle intraparietal sulcus	7/40	-27	-58	43	11.0	497
R inferior occipital gyrus	18	22	-88	-6	10.3	495
R superior temporal gyrus	22	51	-45	15	10.3	486
L inferior occipital gyrus	17	-16	-91	-9	10.2	439
R precentral gyrus	9	38	4	35	9	487
R inferior occipital gyrus	19	39	-82	-6	8.7	470
L inferior occipital gyrus	18	-29	-89	-9	8.5	411
R superior temporal gyrus	42	60	-29	12	8.4	418
L insula	13	-27	-13	23	8.3	460
R fusiform gyrus	37	40	-62	-11	7.9	437
R claustrum	13	38	-19	1	7.7	294
R middle intraparietal sulcus	7/19	29	-62	37	7.7	417
L middle occipital gyrus	18	-28	-85	6	7.6	438
L fusiform gyrus	37	-34	-49	-19	7.5	337
L anterior intraparietal sulcus	7/40	-34	-47	37	7.5	453
R middle temporal gyrus	37	49	-51	-6	7.4	398
R middle temporal gyrus	21	48	-32	-2	7.4	404
R middle temporal gyrus	19	41	-59	11	7.4	481
L posterior cingulate	30	-6	-60	14	7.2	457
L inferior occipital gyrus	19	-39	-76	0	7.2	463
R superior temporal gyrus	22	58	-13	3	7	428

R precuneus	31	29	-74	25	7	377
L claustrum	13	-38	-23	2	6.9	287
L precuneus	31	-28	-73	24	6.9	336
R posterior intraparietal sulcus	7	32	-64	47	6.9	352
R transverse temporal gyrus	41	44	-25	10	6.8	395
pre-supplementary motor area	6	-8	6	54	6.8	256
R cerebellum	*	32	-60	-20	6.6	399
L paracentral lobule	31	-2	-18	45	6.6	383

Differential modulation by episodic and semantic preparatory cues was observed in pre-SMA, left anterior IPS, right precuneus, and left FFG (Fig. 3, top row; see Table 6 for statistical results), indicating that these regions were sensitive to the cued task. Preparatory responses in the right middle and posterior IPS (Fig. 3, bottom right) exhibited a similar response pattern, but in these regions preparatory cue differences were non-significant or marginally significant. Preparatory responses in left middle IPS (Fig. 3, bottom left) were robust but equivalent for both cue types. Surprisingly, in regions showing effects of cue type, semantic task cues elicited larger responses than episodic cues. This finding is counterintuitive, given the relative difficulty of episodic retrieval and the involvement of posterior parietal and medial frontal brain regions in prior studies of episodic retrieval. Nevertheless, episodic task cues produced robust modulation from baseline in all of the regions detailed in Fig. 3, suggesting their importance in episodic task preparation.

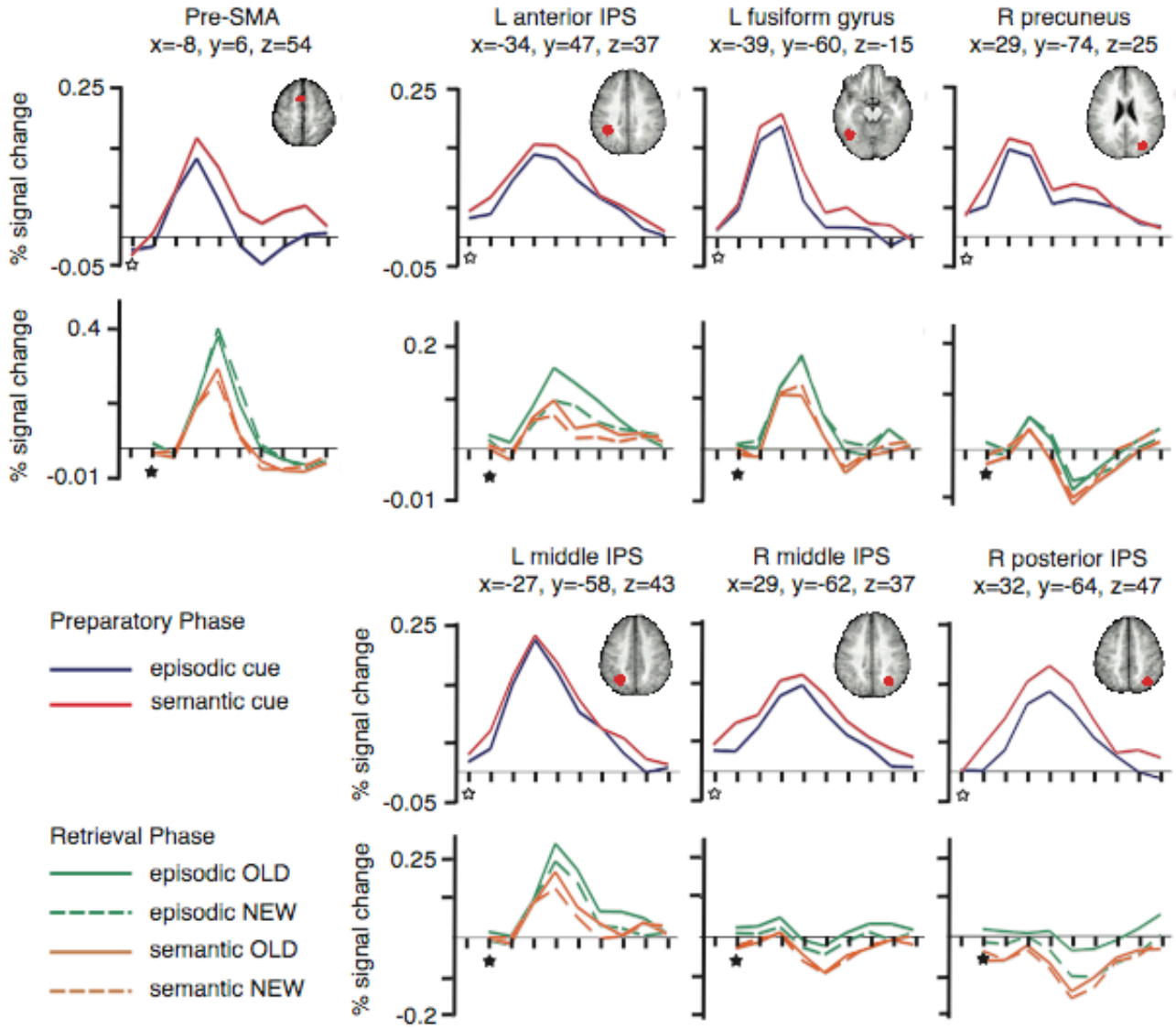

Figure 3. Preparatory phase regions of interest

Regions of interest defined from preparatory phase main effect of time map. Number labels on timecourse plots indicate the occurrence of statistically significant experimental effects (see legend). Top: significant cue-type differences were observed in pre-SMA, left anterior IPS, left FFG, and right precuneus (Table 6). In the retrieval phase, pre-SMA, left anterior IPS, and left FFG displayed significant task differences. Left anterior IPS additionally exhibited old/new differences. Bottom: bilateral middle and right posterior IPS likewise displayed robust cue responses, although cue-type differences were not statistically significant. All three regions exhibited retrieval phase

task differences; additionally, old/new differences were observed in left middle IPS and right posterior IPS. Vertical axis: BOLD signal magnitude as percent change from baseline. Horizontal axis: timecourses extend from 0 to 20 s, beginning from preparatory cue onset; each tick mark corresponds to one 2 s volume of fMRI acquisition. Open stars indicate onset of preparatory cue; closed stars indicate onset of memory probes. Retrieval phase timecourses are based on correct trials only.

3.2.2 Retrieval Phase Activity in Task Preparation Regions

We sought to further characterize regions identified through preparatory phase activity by examining their responses during episodic and semantic retrieval. The pre-SMA, left anterior IPS, left fusiform gyrus, right precuneus (Fig. 3, top row), and left middle IPS (Fig. 3, bottom left) exhibited greater modulation during episodic than semantic retrieval, consistent with the premise that the old/new task required subjects to engage in more controlled processing than the living/non-living task. The right middle and posterior IPS also displayed task differences (Fig 3, bottom right), although these should be interpreted with caution due to apparent baseline differences between timecourses in these regions (note first and last timepoints).

In addition to task differences, both the left anterior and middle IPS exhibited significantly greater responses to old than new items. Notably, these effects were significant in both episodic [left anterior IPS, $t(11)=3.2$, $p<0.01$; left middle IPS, $t(11)=2.8$, $p<0.05$] and semantic [left anterior IPS, $t(11)=3.9$, $p<0.005$; left middle IPS, $t(11)=3.1$, $p<0.01$] retrieval tasks. The right posterior IPS also displayed a main effect of study history; in this region, old/new differences in the episodic task were significant [$t(11)=3.2$, $p<0.05$], while they were not in the semantic task [$t(11)=1.4$, $p<0.2$]. However, baseline differences between timecourses in this region suggest

that old/new effects should be treated with caution. Sensitivity to the study history of memory probes suggests that retrieval phase processing in posterior parietal regions incorporates information from episodic memory.

Although left and right IPS both exhibited positive BOLD modulations in response to preparatory cues, retrieval phase timecourses indicated a dramatic dissociation between these two regions. While left anterior and middle IPS exhibited robust positive responses during episodic and semantic retrieval, activity in both right IPS foci was either negative or not different from baseline, suggesting either inactivity or strategic deactivation of the right IPS during episodic and semantic retrieval. To obtain statistical confirmation of hemispheric differences in the IPS' retrieval phase response profile, we contrasted the combined response of the two left IPS clusters with the combined response of the two right IPS clusters. A 2 x 2 x 2 x 3 ANOVA, comprising factors of region (left/right IPS), task, study history, and time (volumes 4-6) yielded a main effect of region [$F(1,11)=34.9$, $p<0.0001$] and an interaction of region x time [$F(2,22)=7.1$, $p<0.005$]. The heterogeneity of retrieval phase responses in apparently homotopic regions suggests that the role of right IPS in the current paradigm is limited to processing carried out during the preparatory phase of the trial, while left IPS is involved in both preparation and retrieval.

Table 5. Regions defined from retrieval phase main effect of time map

Region	BA	x	y	z	Z-score	Cluster size
L superior frontal gyrus	6	-5	8	52	11.6	407
R cerebellum	*	32	-60	-27	10.1	492
L cuneus	17	-2	-82	8	10.0	478
L superior parietal lobule	7	-30	-60	41	9.7	515
R medial frontal gyrus	6	4	12	47	9.5	305
R inferior occipital gyrus	19	40	-83	-5	9.5	504
R inferior occipital gyrus	18	23	-90	-7	9.1	426
L cerebellum	*	-36	-56	-29	9.1	474
R superior temporal gyrus	22	50	-54	18	9.0	506
L anterior DLPFC	9	-46	17	30	8.8	444
R inferior parietal lobule	40	54	-46	37	8.8	515
R cuneus	23	7	-74	8	8.7	426
L parahippocampal gyrus	30	-10	-48	4	8.7	420
L inferior occipital gyrus	18	-29	-89	-12	8.6	458
R lingual gyrus	18	8	-61	5	8.6	446
L thalamus, medial dorsal nucleus	*	-11	-19	7	8.5	464
L inferior parietal lobule	40	-45	-35	47	8.5	525
L posterior DLPFC	9	-50	5	30	8.5	441
R middle temporal gyrus	21	56	-24	-5	8.3	463
L posterior cingulate	30	-4	-62	11	8.2	418
R parahippocampal gyrus	30	9	-43	1	8.2	424

L supramarginal gyrus	40	-62	-47	37	7.8	225
R thalamus, medial dorsal nucleus	*	11	-19	10	7.7	363
L inferior precuneus	31	-14	-68	25	7.6	431
R caudate head	*	13	9	2	7.4	277
Anterior cingulate	32	-4	22	37	7.3	393
L anterior insula	47	-33	24	2	6.9	465
L superior precuneus	7	-15	-72	47	6.1	332
L inferior parietal lobule	40	-57	-58	40	6.1	186
R anterior insula	45	31	24	5	6.0	257

Table 6. Overview of preparatory and retrieval phase effects

** Reported values are F-statistics from ANOVAs of imaging data, all df=1,11. Statistical significance is denoted by asterisks: *p<0.05, **p<0.001.*

	Preparatory cue differences	Retrieval task differences	OLD/NEW differences
	Regions identified from preparatory phase		
L anterior IPS	7.1*	7.1*	18.9*
Pre-SMA	20.7**	20.5**	0.1; task x hist interaction, F(1,11)=10.1*
L FFG	7.9*	6.6*	1.2
R precuneus	7.0*	4.1	2.3
L middle IPS	1.3	9.4*	16.8*
R middle IPS	1.6	5.8*	3.6
R posterior IPS	3.4	19.1*	14.6*
	Retrieval phase regions displaying OLD/NEW effects		

L inferior precuneus	0.1	39.4**	7.8*; task x hist interaction, F(1,11)=5.1*
L superior precuneus	1.3	20.8**	4.9*
L IPL	0.0	11.3*	65.7**
Retrieval phase regions implicated in attentional control			
L anterior insula	1.0	18.4*	6.5*
R anterior insula	1.7	62.8**	0.1
ACC	0.9	14.3*	0.7
L anterior DLPFC	0.9	1.4	8.9*
L posterior DLPFC	4.1	2.2	1.5
L thalamus, MDN	0.0	6.7*	0.1
R thalamus, MDN	1.7	12.8*	0.1

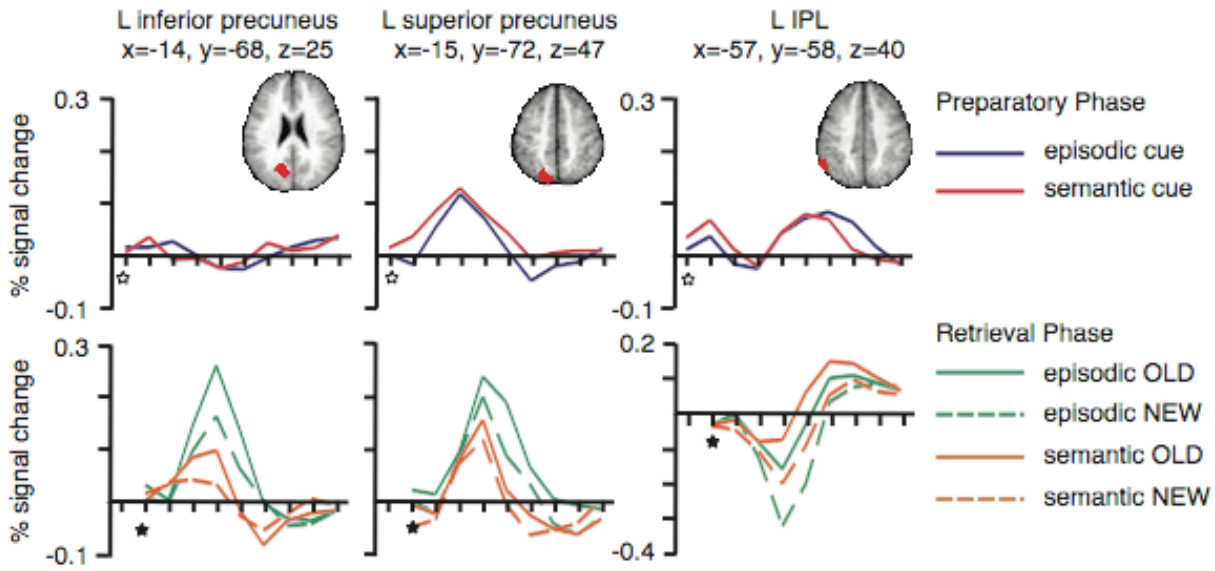

Figure 4. Additional OLD/NEW differences in left parietal retrieval phase regions

Left parietal regions showing old/new differences, identified from retrieval phase main effect of time map. Number labels on timecourse plots indicate the occurrence of statistically significant experimental effects (see legend). Left

inferior precuneus, superior precuneus, and IPL all exhibit significant effects of task and study history in the retrieval phase (Table 6). Vertical axis: BOLD signal magnitude as percent change from baseline. Horizontal axis: timecourses extend from 0 to 20 s, beginning from preparatory cue onset; each tick mark corresponds to one 2 s volume of fMRI acquisition. Open stars indicate onset of preparatory cue; closed stars indicate onset of memory probes. Retrieval phase timecourses are based on correct trials only.

3.2.3 Brain Regions Responding Specifically during Retrieval

The retrieval phase main effect of time map (Fig. 2, bottom panel) revealed a spatial distribution of brain activity which partially overlapped with sites of preparatory phase modulation. Table 5 lists the peak coordinates of 30 regions unique to the retrieval phase map: included are 20 regions displaying the most robust retrieval phase modulation, as well as additional frontoparietal, limbic, and subcortical regions selected on the basis of relevant significant experimental effects. A full list of regions identified by the main effect of time analysis may be obtained from the authors. Retrieval phase modulation was observed in anterior and posterior precuneus activations near the midline, as well as more lateral activations in the inferior parietal lobule and supramarginal gyrus. Activity was also seen in a number of medial and lateral frontal lobe structures, including left dorsolateral prefrontal cortex (DLPFC) and anterior cingulate. Consistent with these activations, bilateral thalamic activations are focused in the medial dorsal nuclei, which innervate multiple regions of prefrontal cortex.

3.2.4 Effects of Study History and Task in Retrieval Phase Regions

Old/new effects were observed in left posterior parietal regions that were undetected by preparatory phase analysis, including ventral and dorsal foci in the precuneus, as well as a focus in the left inferior parietal lobule (IPL; see Fig. 4). In all of these regions, preparatory responses were negligible and insensitive to cue type (Table 6), providing evidence that the function of these regions is limited to processes beginning after onset of the memory probe. As in the left IPS, both precuneus regions exhibited a main effect of study history: old stimuli were associated with significantly greater responses than new stimuli, collapsing across episodic and semantic retrieval tasks (Table 6). Pairwise t-tests indicated that in both precuneus foci, old/new differences were significant only in the episodic task [left superior precuneus, $t(11)=2.5$, $p<0.05$; left inferior precuneus, $t(11)=4.3$, $p<0.01$]. In contrast, responses in the IPL were marked by sharp negative transient responses during the retrieval phase; old/new differences in this region were significant in both episodic and semantic retrieval [$t(11)=4.1$, $p<01$; $t(11)=4.6$, $p<0.001$, respectively]. All three regions displayed significant retrieval phase task effects. In the precuneus, episodic retrieval was associated with larger positive responses than semantic retrieval. Conversely, greater negative modulation was observed in left IPL during episodic than semantic retrieval. The absence of preparatory phase activity in these regions, coupled with robust effects of study history and task in the retrieval phase, suggests that their function is circumscribed to post-stimulus retrieval processes.

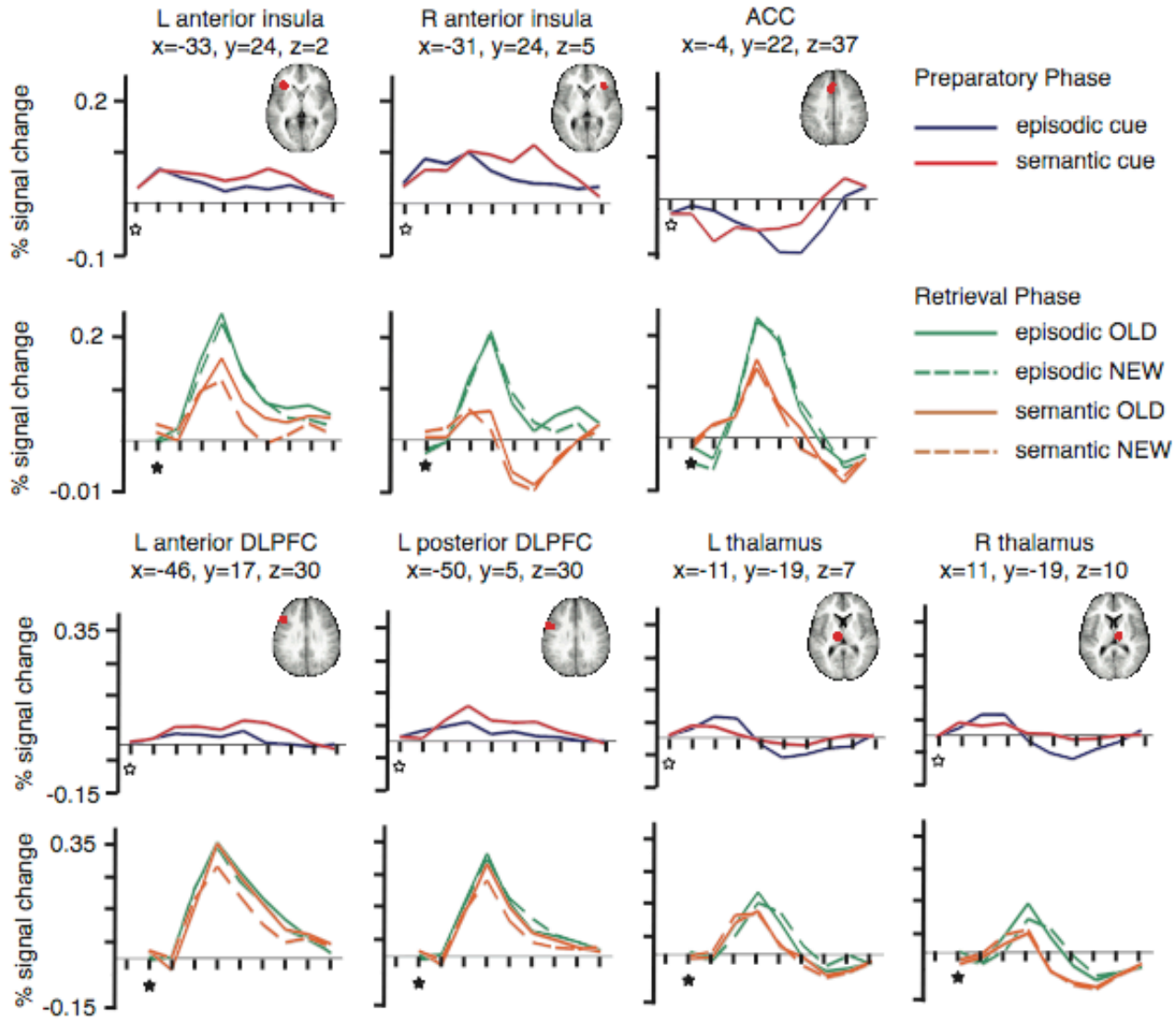

Figure 5. Retrieval phase regions implicated in attentional control

Regions previously implicated in attentional control, identified from retrieval phase main effect of time map. Number labels on timecourse plots indicate the occurrence of statistically significant experimental effects (see legend). All regions except left anterior and posterior DLPFC exhibit significant retrieval phase task differences. Old/new differences occur in left AI and left anterior DLPFC; in all other regions, study history effects are non-significant. Vertical axis: BOLD signal magnitude as percent change from baseline. Horizontal axis: timecourses extend from 0 to 20 s, beginning from preparatory cue onset; each tick mark corresponds to one 2 s volume of fMRI acquisition. Open stars indicate onset of preparatory cue; closed stars indicate onset of memory probes. Retrieval phase timecourses are based on correct trials only.

Episodic and semantic retrieval was also associated with activity in anterior cingulate cortex (ACC), bilateral anterior insula (AI), left DLPFC, and bilateral thalamus (timecourses, Fig. 5; see Table 5 for statistical results). Preparatory responses were small and insensitive to cue type (Table 6), suggesting that these regions are involved in cognitive operations beginning after onset of the memory probe. Importantly, DLPFC, ACC, and AI have been repeatedly implicated in attention and cognitive control (Chein and Schneider, 2005; Cole and Schneider, 2007; Dosenbach et al., 2007, 2008). Retrieval phase responses in these regions and bilateral thalamus were greater for episodic than semantic retrieval, consistent with the exercise of controlled processing during episodic retrieval. Notably, task effects were absent in both anterior and posterior left DLPFC foci (Fig. 5, bottom left panels).

In contrast to the left parietal ROIs described above, activity in these attentional control regions was largely insensitive to stimulus study history. Exceptions to this pattern occurred in left AI and anterior DLPFC (Fig. 5, left panels). Both regions displayed a main effect of study history (Table 6), raising the possibility that these regions interact with retrieved memory content in decision-making processes. Post-hoc t-tests indicated that these differences were significant only during semantic retrieval [insula, $t(11)=3.3$, $p<0.01$; DLPFC, $t(11)=2.4$, $p<0.05$].

4.0 DISCUSSION

If attentional control processes are as integral to the processing of internal mnemonic representations as they are to processing external perceptual representations (Griffin and Nobre, 2003; Nobre et al., 2004), a full model of episodic memory must specify the neural substrates of attentional processes engaged during retrieval. In the current study, separation of task preparation and memory retrieval trial components allowed the dissociation of brain activity related to attentional control from activity associated with processing of internal mnemonic representation. Our findings indicate that preparation to engage in episodic retrieval recruits brain areas associated with domain-general attentional control (Chein and Schneider, 2005; Cole and Schneider, 2007; Dosenbach et al., 2006, 2007, 2008). While preparation to retrieve engaged bilateral parietal cortex, only left parietal regions were active during memory retrieval. Left anterior IPS, which has been separately implicated in attentional control and in episodic retrieval, displayed both preparatory effects and sensitivity to stimulus study history. These findings suggest that left IPS is uniquely involved both in task preparation and memory retrieval.

4.1 TASK PREPARATION RECRUITS DOMAIN GENERAL ATTENTIONAL NETWORK

Preparation to perform either episodic or semantic retrieval involved activation of regions in or near bilateral posterior parietal, IPS, inferior temporal, and occipital lobes, as well as right frontal and right posterior superior temporal cortex (Fig. 2). These modulations are likely to include regions which are involved in low-level processing of cues, such as primary visual cortex, as well as regions which are sensitive to cue type and are engaged in preparing an appropriate task set.

Given our interest in task preparation, we focused on regions differentially modulated by episodic and semantic cues. Cue type effects were found in pre-SMA, left anterior IPS, left FFG, and right precuneus (Fig. 3); similar but non-significant trends were observed in right middle and posterior IPS. In previous fMRI studies of cognitive control, similar sets of brain regions have been associated with responses to task instructions (Dosenbach et al., 2006, 2007) and with practice-related decreases through task learning (Chein and Schneider, 2005). IPS and precuneus activations are also consistent with fMRI results from Wheeler et al. (2006), who report that preparatory cues signaling the study modality of retrieval targets influenced activity in bilateral posterior parietal cortex. In relation to previous ERP studies of episodic retrieval mode, the engagement of bilateral parietal cortex is most consistent with Morcom and Rugg (2002), who reported differential cue-type responses with over both centro-parietal and frontal electrode sites.

Regions differentially modulated by preparatory cues consistently and unexpectedly exhibited greater responses to semantic than episodic task cues. It is possible that study

instructions to encode stimuli for a later memory test biased participants towards episodic task performance, resulting in the need for greater control during semantic task preparation. However, this interpretation must be considered in light of behavioral results, which indicate that participants found the episodic task more difficult. Lower accuracy and higher RTs suggest a need for enhanced control during episodic task preparation, and would lead one to expect greater neural responses to episodic task cues. The absence of a response congruency effect in semantic task RTs is likewise inconsistent with the proposal that participants were biased toward performing episodic retrieval, as RT data showed no evidence that the episodic task set intruded upon semantic retrieval decisions. An alternative explanation of cue type differences involves the degree of success which participants might experience in preparing for both retrieval tasks. In anticipation of a living/non-living decision, participants could shift attention to conceptual knowledge or mental imagery related to animacy; however, an old/new recognition memory decision might not offer an analogous chance to prepare before the presentation of a specific memory probe. This asymmetry in participants' ability to prepare would thus give rise to the observed pattern of cue type effects.

4.2 RETRIEVAL SUCCESS EFFECTS IN LEFT PARIETAL CORTEX

Retrieval phase effects of study history (correct old > new) implicate left IPS (Fig. 3) and adjacent subregions of left parietal cortex (Fig. 4) in an episodic retrieval network. Greater responses to old than new stimuli in left IPS and precuneus replicate similar findings in several

recent fMRI investigations of recognition memory (Buckner et al., 1998c; Donaldson et al., 2001b; Henson et al., 1999; Konishi et al., 2000; Velanova et al., 2003; Wagner et al., 2005). Interestingly, in the semantic task the left IPS and IPL were more active for old than new items (Fig. 3, bottom left; Fig. 4, bottom right) despite the fact that differentiating old and new items was unnecessary. While it appears likely that subjects did not consistently make explicit old/new decisions on semantic trials, it is possible that studied words nevertheless evoked an automatic familiarity signal that was greater in strength than new words. This possibility would be consistent with a strength or familiarity-based hypothesis for the role of left IPS and IPL in memory decisions (Wheeler and Buckner, 2003; Kahn et al, 2004; Wagner et al., 2005). However, another plausible alternative is that items with greater strength of familiarity (which may be mediated elsewhere, such as perirhinal cortex) more effectively engage parietal attentional resources.

4.3 LEFT IPS PARTICIPATES IN BOTH CONTROL AND RETRIEVAL-RELATED PROCESSES

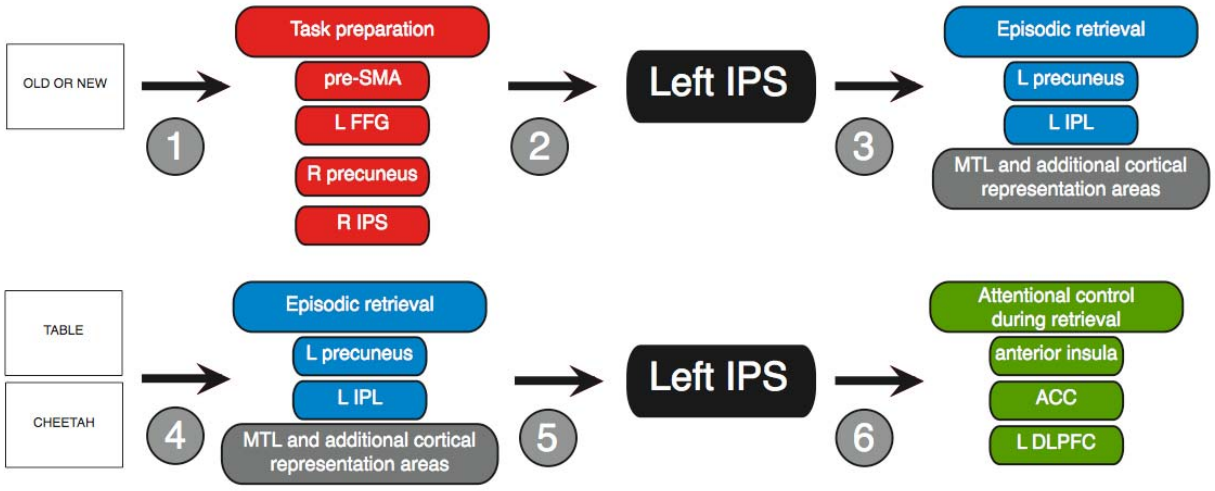

Figure 6. A hypothetical account of left IPS function in episodic retrieval

Preparatory and retrieval phase effects may indicate that left IPS acts as a channel for bidirectional communication between brain systems of attentional control and episodic retrieval. (1) Preparatory cues elicit activity in attentional control regions involved in task-level preparation, including implementation of appropriate task goals, decision criteria, and response options. (2)-(3) Preparatory regions transmit a biasing signal to regions involved in representation and retrieval of episodic content. The modulatory influence of this signal in advance of a memory probe could facilitate subsequent retrieval. (4) Memory probes are compared to episodic memory traces to assess whether an item is OLD or NEW. (5)-(6) The results of retrieval are transmitted via left IPS to attentional control regions involved in decision-making and response processes.

While several brain regions were positively modulated during both preparatory and retrieval phases, left IPS was the only region sensitive to both cue type and the study history of memory probes. This region thus represents a point of overlap between task preparation and

memory retrieval effects. Fig. 6 presents one possible functional account of these effects, in which left IPS acts as a channel for bidirectional communication between a top-down attentional control system and brain regions subserving episodic memory.

Previous research has suggested that parietal cortex is a source of biasing signals to external and internal representations (Anderson et al., 2004; Corbetta and Shulman, 2002; Desimone and Duncan, 1995; Wagner et al., 2005). Given this evidence, it is possible that preparatory phase effects indicate a biasing signal that shifts attention to internal memory representations and disposes the subject to apply an appropriate task set (Fig. 6, steps 1-3). Connectivity analyses suggest the existence of such a channel between the parietal lobes and medial temporal lobe memory areas (Vincent et al., 2006).

During the retrieval phase of the trial, left IPS might also permit the return of information from episodic and semantic memory to control areas, possibly including areas involved in decision-making and response (Fig. 6, steps 4-6). The expression of retrieved content in parietal cortex is similar to Wagner et al.'s (2005) "output buffer" theory, according to which information retrieved from memory would be instantiated by the firing patterns of parietal neurons. The level of parietal activity would probably also vary according to the study history of stimuli, giving rise to retrieval success effects. The bidirectional flow of information depicted in Fig. 6 makes an appealing analogy to visual attention studies in non-human primates, which indicate that top-down and bottom-up influences converge in parietal cortex to form a spatial map of behaviorally relevant stimuli (Balan and Gottlieb, 2007; Colby and Goldberg, 1999).

The hypothetical flow of attentional biasing signals and retrieved information in this channel model suggests ways to experimentally test its validity. If left IPS represents a critical

conduit for communications between attentional control and memory retrieval systems, interruption of its function might result in spared performance on memory retrieval tasks which minimally tax attention, coupled with impaired performance on paradigms which stress attentional control (e.g., when subjects must switch between tasks or retrieval sets or perform exhaustive memory searches). In practice, however, designing a paradigm which causally links memory performance, attentional control, and the integrity of parietal function represents a significant challenge.

4.4 RETRIEVAL PHASE ACTIVITY DISSOCIATES LEFT AND RIGHT IPS

While left and right IPS are both positively modulated by preparatory cues signaling episodic and semantic retrieval, they respond differentially during retrieval itself. The left anterior (x=-34, y=-47, z=37) and middle IPS (x=-27, y=-58, z=43) exhibited positive transient responses in the retrieval phase and were more active on correct old than new trials (Fig.3). These regions are located near parietal areas that are commonly associated with successful retrieval in recognition memory studies (Buckner and Wheeler, 2001; Rugg and Wilding, 2000; Wagner et al., 2005). In contrast, the right IPS was negatively modulated during task performance. This retrieval-phase dissociation of left and right IPS is consistent with left lateralization of retrieval success effects, which cannot be attributed to the use of verbal stimuli (Sanefuji et al., 2007). It is unclear whether the negative response in right IPS indicates a strategic deactivation of this region, or a mere lack of functional relevance to the retrieval tasks which we employed.

4.5 RETRIEVAL PHASE MODULATES ACTIVITY IN ADDITIONAL CONTROL AREAS

We additionally identified retrieval phase activity in a set of brain regions, including left DLPFC, bilateral AI, thalamus, and ACC (Fig. 5). In contrast to task preparation regions like the left FFG and bilateral IPS, these regions displayed negligible preparatory responses. Thus, they do not participate in anticipatory task-level processing such as the preparation of the appropriate task set. Despite robust responses during task performance, many regions of this set were insensitive to the study history of stimuli, suggesting that they are also not involved in retrieval-specific operations. Instead, they may perform control-related functions during retrieval, such as decision making or response selection and execution. For example, the modulation of attentional control during retrieval is supported by Dobbins et al. (2002), who reported activation in left DLPFC and left inferior prefrontal cortex during both source and item memory tasks. Dobbins et al. observed greater responses in these regions during the source memory task, which was hypothesized to require higher levels of executive control in cue specification and recollective monitoring. Relatedly, Wheeler and Buckner (2003) demonstrated that increased demands for control during memory retrieval produced increased BOLD responses in multiple brain regions, including bilateral anterior insula and anterior cingulate (see also Velanova et al., 2003).

5.0 CONCLUSION

Human beings benefit greatly from the ability to perform directed, voluntary memory retrieval. Neuroimaging studies of memory demonstrate that this ability depends upon complex interactions among multiple brain regions over time. Our results indicate that preparation for memory retrieval relies on several brain regions previously associated with attentional control, including bilateral parietal cortex. Retrieval itself is associated with the activation of additional attentional control regions, which may participate in decision-making and response processes. Retrieval also produced robust memory effects in left, but not right, parietal cortex. As a region of overlap between preparatory effects and old/new differences, the left IPS may fulfill a complex role encompassing aspects of attentional control and the representation of episodic content. Further research must examine whether a single functional interpretation can explain both attentional and memory-related effects in parietal cortex.

BIBLIOGRAPHY

Anderson, M. C., Ochsner, K. N., Kuhl, B., Cooper, J., Robertson, E., Gabrieli, S. W., et al., Glover, G. H., Gabrieli, J. D. E., 2004. Neural systems underlying the suppression of unwanted memories. Science 303, 232-235.

Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., Corbetta, M., 2003. Functional Organization of Human Intraparietal and Frontal Cortex for Attending, Looking, and Pointing. J. Neurosci. 23, 4689-4699.

Balan, P., Gottlieb, J., 2006. Integration of Exogenous Input into a Dynamic Salience Map Revealed by Perturbing Attention. J. Neurosci. 26, 9239-9249.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Wagner, A. D., Rosen, B. R., 1998a. Functional-anatomic study of episodic retrieval using fMRI. I. Retrieval effort versus retrieval success. NeuroImage 7, 151-62.

Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., Dale, A. M., 1998b. Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. Neuron 20, 285-96.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Dale, A. M., Rotte, M., Rosen, B. R., 1998c. Functional-anatomic study of episodic retrieval. II. Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. NeuroImage 7, 163-75.

Buckner, R. L., Wheeler, M. E., 2001. The cognitive neuroscience of remembering. Nat. Rev. Neurosci. 2, 624-34.

Chein, J. M., Schneider, W., 2005. Neuroimaging studies of practice-related change: fMRI and meta-analytic evidence of a domain-general control network for learning. Cognitive Brain Res. 25, 607-623.

Cohen, J. D., MacWhinney, B., Flatt, M., Provost, J., 1993. PsyScope: An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. Behav. Res. Meth. Ins. C. 25, 257-271.

Colby, C., Goldberg, M., 1999. Space and Attention in Parietal Cortex. Annu. Rev. Neurosci. 22, 319-349.

Cole, M., Schneider, W., 2007. The Cognitive Control Network: Integrated Cortical Regions with Dissociable Functions. NeuroImage 37, 343-360.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al., 1998. A common network of functional areas for attention and eye movements. Neuron 21, 761-773.

Corbetta, M., Kincade, J., Ollinger, J. M., McAvoy, M. P., Shulman, G. L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat. Neurosci. 3, 292-297.

Corbetta, M., Shulman, G., 2002. Control of Goal-Directed and Stimulus-Driven Attention in the Brain. Nat. Rev. Neurosci. 3, 201-215.

Dale, A. M., 1999. Optimal experimental design for event-related fMRI. Hum. Brain Mapp. 8, 109-114.

Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. 18, 193-222.

Dobbins, I. G., Foley, H., Schacter, D. L., Wagner, A. D., 2002. Executive Control during Episodic Retrieval: Multiple Prefrontal Processes Subserve Source Memory. Neuron 35, 989-996.

Dobbins, I. G., Han, S., 2006. Cue- versus Probe-dependent Prefrontal Cortex Activity during Contextual Remembering. J. Cognitive Neurosci. 18, 1439-1452.

Donaldson, D. I., Petersen, S. E., Buckner, R. L., 2001a. Dissociating memory retrieval processes using fMRI: evidence that priming does not support recognition memory. Neuron 31, 1047-59.

Donaldson, D. I., Petersen, S. E., Ollinger, J. M., Buckner, R. L., 2001b. Dissociating state and item components of recognition memory using fMRI. NeuroImage 13, 129-42.

Dosenbach, N. U., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A., et al., 2007. Distinct brain networks for adaptive and stable task control in humans. Proc. Natl. Acad. Sci. U. S. A. 104, 11073-11078.

Dosenbach, N. U. F., Fair, D. A., Cohen, A. L., Schlaggar, B. L., Petersen, S. E., 2008. A dual-networks architecture of top-down control. Trends Cogn. Sci., 12, 99-105.

Dosenbach, N. U. F., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., et al., 2006. A core system for the implementation of task sets. Neuron 50, 799-812.

Düzel, E., Cabeza, R., Picton, T. W., Yonelinas, A. P., Scheich, H., Heinze, H. J., et al., 1999. Task-related and item-related brain processes of memory retrieval. Proc. Natl. Acad. Sci. U. S. A. 96, 1794-9.

Friston, K. J., Jezzard, P., Turner, R., 1994. Analysis of functional MRI time-series. Hum. Brain Mapp., 153-171.

Griffin, I. C., Nobre, A. C., 2003. Orientational attention to locations in internal representations. J. Cognitive Neurosci. 15, 1176-1194.

Henson, R. N., Rugg, M., Shallice, T., Josephs, O., Dolan, R., 1999. Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. J. Neurosci. 19, 3962-3972.

Herron, J. E., Wilding, E. L., 2004. An electrophysiological dissociation of retrieval mode and retrieval orientation. NeuroImage 22, 1554-62.

Herron, J. E., Wilding, E. L., 2006. Brain and behavioral indices of retrieval mode. NeuroImage 32, 863-70.

Jacoby, L. L., Bishara, A. J., Hessels, S., Toth, J. P., 2005. Aging, Subjective Experience, and Cognitive Control: Dramatic False Remembering by Older Adults. J. Exp. Psychol. Gen. 134, 131-148.

Kahn, I., Davachi, L., Wagner, A. D., 2004. Functional neuroanatomic correlates of recollection: Implications for models of recognition memory. J. Neurosci. 24, 4172-4180.

Konishi, S., Wheeler, M. E., Donaldson, D. I., Buckner, R. L., 2000. Neural correlates of episodic retrieval success. NeuroImage 12, 276-86.

Kucera, H., Francis, W. N., 1967. Computational Analysis of Present-Day American English. Brown University Press, Providence.

Kusunoki, M., Gottlieb, J., Goldberg, M. E., 2000. The lateral intraparietal area as a salience map: The representation of abrupt onset, stimulus motion, and task relevance. Vision Res. 40, 1459-68.

Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weisskoff, R. M., Poncelet, B. P., et al., 1992. Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. Proc. Natl. Acad. Sci. U. S. A. 89, 5675-5679.

Lepage, M., Ghaffar, O., Nyberg, L., Tulving, E., 2000. Prefrontal cortex and episodic memory retrieval mode. Proc. Natl. Acad. Sci. U. S. A. 97, 506-11.

McAvoy, M. P., Ollinger, J., Buckner, R., 2001. Cluster Size Thresholds for Assessment of Significant Activation in fMRI. NeuroImage 13, S198.

Miezin, F. M., Maccotta, L., Ollinger, J. M., Petersen, S. E., Buckner, R. L., 2000. Characterizing the hemodynamic response: effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. NeuroImage 11, 735-59.

Morcom, A. M., Rugg, M. D., 2002. Getting ready to remember: The neural correlates of task set during recognition memory. Neuroreport 13, 149-52.

Nobre, A. C., Coull, J., Maquet, P., Frith, C., Vandenberghe, R., Mesulam, M., 2004. Orienting Attention to Locations in Perceptual Versus Mental Representations. J. Cognitive Neurosci. 16, 363-73.

Nyberg, L., Cabeza, R., Tulving, E., 1996. PET studies of encoding and retrieval: The HERA model. Psychon. B. Rev. 3, 135-148.

Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., et al., 1992. Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. Proc. Natl. Acad. Sci. U. S. A. 89, 5951-5955.

Ojemann, J. G., Akbudak, E., Snyder, A. Z., McKinstry, R. C., Raichle, M. E., Conturo, T. E., 1997. Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. NeuroImage 6, 156-167.

Ollinger, J. M., Corbetta, M., Shulman, G. L., 2001a. Separating processes within a trial in event-related functional MRI. NeuroImage 13, 218-29.

Ollinger, J. M., Shulman, G. L., Corbetta, M., 2001b. Separating processes within a trial in event-related functional MRI. NeuroImage 13, 210-7.

Rugg, M. D., Wilding, E. L., 2000. Retrieval Processing and Episodic Memory. Trends Cogn. Sci. 4, 108-115.

Sanefuji, M., Nakashima, T., Kira, R., Iwayama, M., Torisu, H., Sakai, Y., et al., 2007. The relationship between retrieval success and task performance during the recognition of meaningless shapes: an event-related near-infrared spectroscopy study. Neurosci. Res., 59, 191-198.

Shulman, G. L., d'Avossa, G., Tansy, A. P., Corbetta, M., 2002. Two attentional processes in the parietal lobe. Cereb. Cortex 12, 1124-1131.

Snyder, A. Z., 1996. Difference Image Versus Ratio Image Error Function Forms in PET-PET Realignment. In: Bailey, D., Jones, T. (Eds.), Quantification of Brain Function Using PET. Academic Press, San Diego.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme Medical Publishers, Inc., New York.

Tulving, E. , 1983. Elements of Episodic Memory. New York, Oxford University Press.

Tulving, E., 2004. How Many Memory Systems Are There? In: Balota, D. A., Marsh, E. J. (Eds.), Cognitive psychology: Key readings. Psychology Press, United Kingdom.

Velanova, K., Jacoby, L. L., Wheeler, M. E., McAvoy, M. P., Petersen, S. E., Buckner, R. L., 2003. Functional-Anatomic Correlates of Sustained and Transient Processing Components Engaged during Controlled Retrieval. J. Neurosci. 23, 8460-8470.

Velanova, K., Lustig, C., Jacoby, L. L., Buckner, R. L., 2007. Evidence for frontally mediated controlled processing differences in older adults. Cereb. Cortex 17, 1033-1046.

Vincent, J. L., Snyder, A. Z., Fox, M. D., Shannon, B. J., Andrews, J. R., Raichle, M. E., et al., 2006. Coherent spontaneous activity identifies a hippocampal-parietal memory network. J. Neurophysiol. 96, 3517-3531.

Wagner, A. D., Shannon, B. J., Kahn, I., Buckner, R. L., 2005. Parietal lobe contributions to episodic memory retrieval. Trends Cogn. Sci. 9, 445-453.

Werkle-Bergner, M., Mecklinger, A., Kray, J., Meyer, P., Duzel, E., 2005. The control of memory retrieval: Insights from event-related potentials. Cognitive Brain Res. 24, 599-614.

Wheeler, M. E., Buckner, R. L., 2003. Functional Dissociation among Components of Remembering: Control, Perceived Oldness, and Content. J. Neurosci. 23, 3869-3880.

Wheeler, M. E., Buckner, R. L., 2004. Functional-anatomic correlates of remembering and knowing. NeuroImage 21, 1337-49.

Wheeler, M. E., Shulman, G. L., Buckner, R. L., Miezin, F. M., Velanova, K., Petersen, S. E., 2006. Evidence for separate perceptual reactivation and search processes during remembering. Cereb. Cortex 16, 949-59.